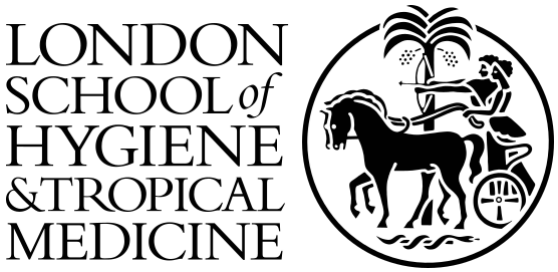

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Introduction

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Understanding variation in human fertility: what can we learn from evolutionary demography?

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Decades of research on human fertility has presented a clear picture of *how* fertility varies, including its dramatic decline over the last two centuries in most parts of the world. *Why* fertility varies, both between and within populations, is not nearly so well understood. Fertility is a complex phenomenon, partly physiologically and partly behaviourally determined, thus an interdisciplinary approach is required to understand it. Evolutionary demographers have focused on human fertility since the 1980s. The first wave of evolutionary demographic research made major theoretical and empirical advances, investigating variation in fertility primarily in terms of fitness maximization. Research focused particularly on variation within high-fertility populations and small-scale subsistence societies and also yielded a number of hypotheses for why fitness maximization seems to break down as fertility declines during the demographic transition. A second wave of evolutionary demography research on fertility is now underway, paying much more attention to the cultural and psychological mechanisms underpinning fertility. It is also engaging with the complex, multi-causal nature of fertility variation, and with understanding fertility in complex modern and transitioning societies. Here, we summarize the history of evolutionary demographic work on human fertility, describe the current state of the field, and suggest future directions.

1. Introduction

Human fertility is highly variable (figure 1).[1] The highest recorded fertility for any population in human history belongs to the Hutterites, a North American Anabaptist religious sect where, in the early twentieth century, married women managed a remarkable average of almost 11 children each [2]. This contrasts with recent fertility rates approaching just one child per women in some East Asian populations[2]: Taiwan currently has the lowest national fertility rate of 1.1 children per woman [3]. These population-level averages, though divergent, are dwarfed in comparison to individual-level variation in fertility. In some Western European countries, a quarter of women remain childless, a characteristic of this world region which extends back at least a couple of centuries [4]. Yet *The Guinness Book of World Records 1998* claims one 18th century Russian woman gave birth to 69 children [5], and there are historical accounts of powerful men fathering close to 1000 children [6,7]. The timing of childbearing also varies dramatically. An average age at first birth in the late teens for women was probably the case throughout most of human history, and still is in some societies. But the current average age at first birth for women in the European Union is 29 years, meaning that women wait half of their potential reproductive lifespans before having their first child.[3]

How can we account for such variation? Fertility is clearly a very complex trait, both physiologically and behaviourally determined. The total number of children a woman ends up with depends on a number of pivotal 'decisions':

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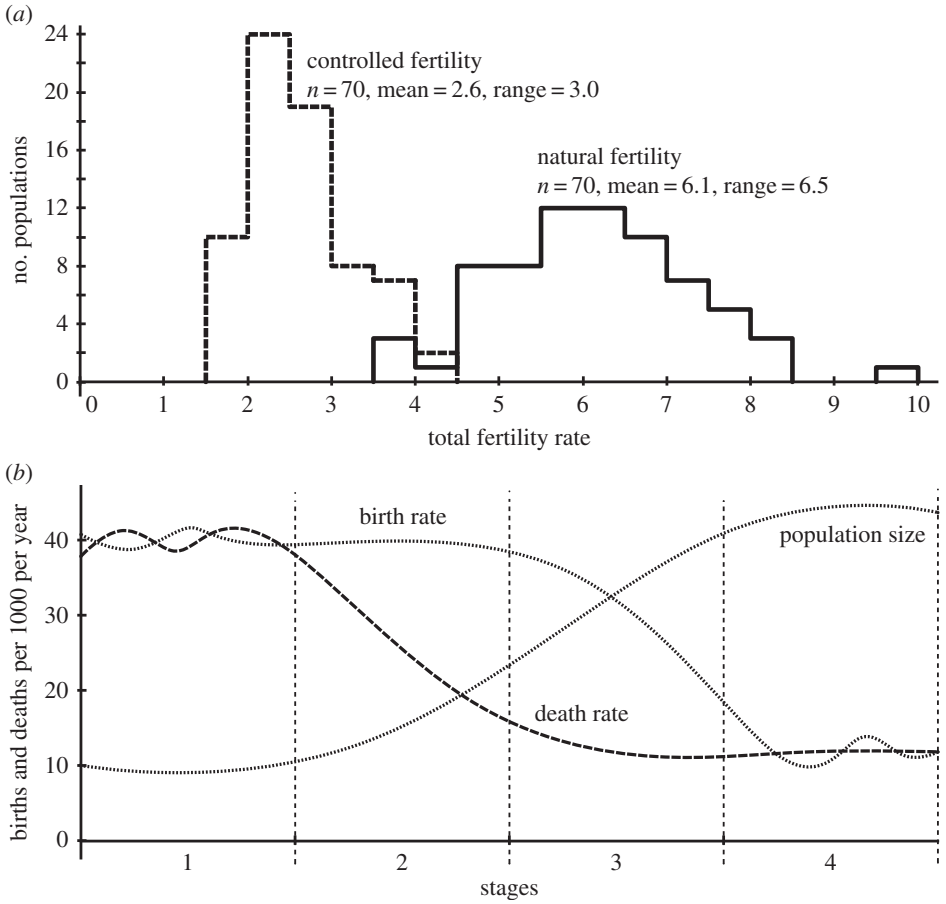

Figure 1. Variation in human fertility. (*a*) Distribution of total fertility rates or mean completed family sizes in 70 natural-fertility populations (solid line) and 70 controlled-fertility populations (dashed line). Note that natural fertility populations are highly variable. In fact, the range in fertility rates observed in natural fertility populations exceeds the difference between the mean fertility rates observed in natural versus controlled settings. Figure redrawn from [1, p. 48]. Populations known to have high prevalences of pathological sterility are excluded. (*b*) A schematic of the 'Demographic Transition Model', which describes the typical demographic shifts observed as populations undergo development from a pre-industrial to industrialized economic system. In stage one, total population is low and stable due to high birth rates and high death rates. In stage two, total population rises as death rates fall following improvements in healthcare and sanitation. Birth rates remain high. In stage three, total population is still rising rapidly, but fertility falls, narrowing the gap between birth and death rates. In stage four, population growth stabilizes, balanced by a low birth rate and a low death rate.

whether to have children at all and, if so, when to have the first child, whether and when to have subsequent children, and when to stop. Such decisions may be taken by a woman's physiology, since sufficient energetic reserves need to be available for successful reproduction. As does a partner, at least in the absence of assisted reproductive technology. Consequently, direct fertility decisions are also interwoven with more distal decisions about whether and when to partner, who to partner with, whether to dissolve a partnership, and whether and when to re-partner after dissolution. Fertility decisions will therefore be influenced by both the physiological condition and behavioural strategies of that partner. To add further complexity, in our social species, fertility is influenced by other individuals, including the availability and behaviour of our family and friends, wider social norms surrounding reproduction, and institutional factors which influence many aspects of fertility, family and work life, essentially providing the option set of strategies available to individuals within a social context. With so many 'moving parts', it is unsurprising that theories of fertility are diverse.

Studying reproductive decision-making in humans, unlike other species, offers the advantage that we can ask our subjects about why they make the decisions they do. Yet this advantage offers a false head-start: individuals can behave in ways which may increase or decrease fertility without conscious strategizing. The evidence is mixed on the extent to which fertility decisions are consciously determined. The existence of contraception and abortion throughout recorded history is clear evidence for a desire to control fertility under at least some circumstances [8]. Bledsoe's ethnographic research in the Gambia also suggests that couples in small-scale societies engage in very active conscious strategizing about reproductive timing in order not to have births that are too closely spaced [9]. On the other hand, Fisher's qualitative research reconstructing British couples' attitudes towards fertility limitation during the early 20th century suggests a distinct lack of such joint deliberation [10]. Further, women in low-fertility countries who have good access to contraception and (in most populations) abortion seem surprisingly inaccurate at controlling their fertility. Estimates for the proportion of pregnancies which are unplanned are high in such populations, approaching half of all pregnancies in both Europe and the US (e.g. [11]). But in addition to this unplanned fertility, women in low-fertility populations tend to state preferences for more children than they actually end up having, a phenomenon often referred to as an 'unmet need for children' [12], which suggests a failure to implement fertility desires. Conscious strategizing may therefore play a limited role with respect to the reproductive decision-making process,

and even where it exists, care needs to be taken over its interpretation, as consciousness may in fact be a post hoc rationalization of what individuals have already done.

The social science of demography has engaged with the question of why fertility varies for decades, initially focusing on population-level trends. Theories of the fertility transition (the decline in fertility which has followed, or happened in tandem with, mortality decline and economic development worldwide over the last few centuries: figure 1*b*) extend back to the 1920s [13]. More recently, demographers have attempted to explain population-level phenomena by trying to understand individual behaviour. A vast body of research now exists on fertility, documenting, describing, and partially explaining why fertility varies so much between populations and between individuals. Yet no holistic, comprehensive understanding of why fertility varies has been reached. As a result, fertility is still surprisingly hard to predict. A number of unexpected fluctuations in fertility have occurred in high-income populations since the Second World War (WWII): from the sustained surge in fertility or 'baby boom' in the immediate post-war decades, to a sharp decline in fertility throughout the 1970s to below replacement levels, to recent upticks in fertility in some high-income populations [14]. Fertility change in low- and middle-income populations has been similarly unpredictable: fertility declines in some parts of Asia and Latin America occurred faster than anticipated, and there has been unanticipated stalling in the fertility decline in some sub-Saharan African populations [15].

As is increasingly recognized in the demographic literature, an interdisciplinary approach is needed to help us understand fertility variation in all its complexity. Demography has an unusual relationship with theory, as it is defined by the phenomena under study, rather than any particular explanatory framework used by demographers [16–18]. The best-known demographic theory—'Demographic Transition Theory'—, for example, is infamously not a causal theory at all, but rather a descriptive account of the changes in fertility and mortality which typically accompany economic development. This theoretical agnosticism is actually beneficial in many ways, in that it has freed the discipline to draw on multiple alternative disciplines and theoretical frameworks to help explain demographic phenomena, mostly involving other social sciences, particularly sociology and economics ([19]—at least in the post-WWII period; pre-WWII demography and biology were closely entwined [20]). This interdisciplinarity has led to a useful and diverse body of work exploring why fertility varies, and has helped to generate alternative hypotheses which can be tested against or in concert with one another. The European Fertility Project [21], for example, aimed to test economic versus sociological models of the demographic transition against each other.

It has only been relatively recently, however, that concerted attempts have been made to inform demographic thinking with concepts from the natural sciences. Today, the subfield of evolutionary demography is gaining ground, driven by the acknowledgement of researchers from both natural and social sciences that natural and social phenomena are interrelated, and thus combining these approaches is essential for a holistic explanation of demographic patterns [22–24]. Here, we outline the key aims and assumption of the evolutionary demography paradigm, highlighting the advances made during what we describe as the 'first wave' of evolutionary demography research on fertility that occurred during the 1980s and 1990s. We also use this section to highlight the differences between evolutionary and non-evolutionary, or 'conventional', demographic research on fertility. Throughout this review, we refer to conventional demography as what we perceive to be widely shared opinions among many demographers on the particular topic that we discuss, while acknowledging that demography is a large and varied discipline, so that there is no single conventional demographic view. This discussion inevitably makes generalizations about both conventional and evolutionary demography; both disciplines are much more nuanced than this brief overview suggests, but we consider that such high-level summaries can be very useful in aiding interdisciplinary conversations by highlighting key similarities and differences between fields. We further emphasize that evolutionary and other approaches to demography are complementary, and rather than being viewed as alternatives should instead be seen as historically separate perspectives which have much to contribute to each other. We then go on to consider how contemporary research in evolutionary demography (or the 'second wave') has changed focus and is making advances in new areas of research on fertility, while highlighting the research reviewed and presented in this special issue.

2. The first wave

Evolutionary demography is the application of theory from evolutionary biology to demographic phenomena (fertility, mortality and migration). In the context of fertility, life-history theory and parental investment theory are the evolutionary theories most commonly used [25,26]. In some regards, evolutionary demography can be thought of as a hybrid discipline, somewhere in between the natural and social sciences. It sometimes adopts the 'top-down' approach of the natural science of evolutionary biology, by testing specific hypotheses derived from evolutionary theory (such as 'is economic success correlated with reproductive success?', based on the hypothesis from life-history theory that natural selection has designed individuals to convert resources into offspring). But, unlike evolutionary biology, evolutionary demography also frequently adopts the 'bottom-up' or 'object science' approach of the social science of demography, which seeks to explain a particular phenomenon (such as 'why does fertility vary?'). To date, evolutionary demography is perhaps better known for its work on mortality, as there has been a successful and sustained programme of research which aims to further our understanding of mortality patterns and aging using an evolutionary, cross-species approach [27]. As this suggests, evolutionary demography is a discipline which is interested in all species and has produced fascinating work on how mortality and fertility rates vary between species (e.g. [28]). Here, however, we focus exclusively on intra-species variation in human fertility.

(a) The start of the first wave

One of the earliest evolutionary demographic studies, Blurton-Jones's 'backload model', tested the hypothesis that the length of the birth intervals of !Kung hunter-gatherers allowed women to balance optimally the energetic demands of child-bearing and foraging in a society where women had to carry small children and foraged foods substantial distances [29]. The assumption underlying this backload model is that the

ultimate aim of birth intervals is to maximize child survival and therefore evolutionary fitness (genetic representation in future generations). This ultimate layer of explanation distinguishes evolutionary models from social science models, which typically focus on 'proximate explanations', i.e. the mechanisms which bring behaviour about. Note that, throughout, we use 'proximate' in the evolutionary, not demographic, sense. In demography, proximate determinants of fertility are the direct biological and behavioural influences on fertility through which the 'distal' determinants of social, economic, and cultural factors act ([30]; for example, the distal determinant of education may influence fertility through the proximate deteminants of delayed marriage and higher contraceptive use). In evolutionary terminology, both demographic proximate and distal determinants would be considered proximate explanations, since both are explanations for *how* fertility is brought about. Neither of these types of explanations address *why* these determinants influence fertility, since in evolutionary biology this needs an 'ultimate' (also sometimes known as a 'functional') explanation, in terms of fitness maximization [31].[4]

The driving force behind evolutionary demography work during the first wave was often a concern with ultimate explanations of fertility variation, typically starting with the prediction that fertility broadly functions to maximize fitness in a particular ecology. This means that, though proximate explanations were not ignored, they were not often the primary focus of first wave work. For example, the substantial body of work which demonstrated clear positive relationships between wealth and fertility for both men and women (at least in high fertility societies) derived from the life-history prediction that individuals should use their resources in order to increase reproductive success (reviewed in [32]). Determining exactly how economic success led to reproductive success was often a secondary concern in such studies. Note that this means that evolutionary and non-evolutionary demographic explanations for fertility are often entirely compatible, with evolutionary demography adding a complementary layer of explanation (in terms of fitness maximization) to social science approaches focused on understanding the proximate explanations of fertility [22]. This difference in focus—ultimate versus proximate explanations—is no doubt one reason early evolutionary demography did not make a significant dent on the consciousness of conventional demography, but there are some other differences in the aims of the two strands of demography which may have limited cross-fertilization.

One of the strong emphases of first wave evolutionary demography, due to its roots in anthropology, was in explaining variation within societies with careful attention to the ethnographic context in which fertility outcomes were realized. Much first wave work on fertility therefore focused on understanding individual-level variation in fertility in small-scale, high-fertility societies (sometimes referred to by demographers as 'natural-fertility' populations) (but see [33,34]). This focus was influenced, in part, by the desire of evolutionary researchers to understand the evolutionary history of the human species. This emphasis on small-scale societies, especially hunter-gatherers but also subsistence agricultural, horticultural and pastoral populations (both contemporary and historical [35]), has been a real strength of the discipline and provides a detailed window onto the wide diversity of human fertility experiences. First wave research largely interpreted the number of children a woman produces in such societies as the result of adaptations that calibrate fertility to a particular local socio-ecology, taking into account the woman's individual 'state' or condition. Variation in fertility is therefore a function of differences in socio-ecology and differences in individual condition. Socio-ecology refers to both the physical and social environment, including cultural institutions (e.g. marriage or inheritance system), which are at least sometimes conceived of in this research as part of the ecology to which fertility adapts (but see [36,37] for examples of evolutionary work where cultural institutions are the focus of enquiry). First wave work was therefore somewhat different in focus than more conventional demographic approaches, which have shown interest in investigating fertility in all kinds of human population, though with a particular emphasis (at least in contemporary demography) on analysis at the level of the nation-state.

(b) The physiological regulation of fertility

Though the driving force behind evolutionary demographic investigations is an interest in ultimate explanations, evolutionary demography has contributed quite substantially to the study of proximate explanations in one particular area: the role of energetic status in physiologically determining fertility. For example, Blurton-Jones's [29] model described above assumes that energetic status influenced by backload is the proximate determinant of birth spacing. Many evolutionary demographers make the assumption that throughout most of human history physiological mechanisms would probably have been of paramount importance in determining fertility (rather than any behavioural manipulation of fertility). In fact, the new sub-discipline of reproductive ecology emerged in the 1990s. This is an evolutionary discipline which has explored relationships between energetic status and reproductive physiology, particularly via hormonal mechanisms [38–40]. Reproductive ecologists have now clearly demonstrated that reproductive physiology responds to energetic flux—not just the availability of energy but also energetic expenditure—and have proposed that these are adaptive responses that calibrate reproduction to the local environment. Under conditions of energetic stress, reproduction should be downregulated to avoid attempting a reproductive bout which is likely to end in costly failure. In contrast, conventional demography has paid less attention to the purely physiological adjustment of fecundity to energetic status, and a few demographers have even been rather sceptical of the claim that energetic status has a significant impact on fertility [1,41]. These demographers have argued that, despite the evidence that reproductive physiology may respond to energetic status, there is much less evidence that fertility itself is strongly limited by energy balance, except under extreme circumstances. This perspective may partly stem from the observation that little between-population variation in fertility can be attributed to energetic status, at least in contemporary societies, where the most energetically constrained populations clearly have the highest fertility.

(c) The behavioural regulation of fertility

The conventional demographic literature has focused largely on the behavioural mechanisms which influence fertility. The heuristics used to guide some of this work are also somewhat different from those used in evolutionary demography: rather than starting with the prediction that natural selection

optimally matches fertility to the local ecology in natural fertility societies, conventional demography has instead posed the question, 'why are high birth rates so low?' [42]. This question arises from the 'proximate determinants of fertility' framework, which suggests that fertility is surprisingly low in natural-fertility populations because it is below the physiological maximum which can be attained [30]. This physiological maximum is thought to be 15 children, which could be produced if women started having babies as soon as they were physiologically able, continued to reproduce until menopause, and spaced births without any breastfeeding. This is not a heuristic an evolutionist is likely to have come up with, as it assumes no post-partum parental investment, whereas all mammal species are committed to such maternal investment through lactation. This has proved a very useful heuristic in demography, however, as a framework to decompose fertility into separate components. This allows demographers to get a handle on why fertility varies between populations by identifying which proximate determinants vary between populations. Though the proximate determinants include both physiological and behavioural factors, in fact, the proximate determinants thought to have most power to explain variation in fertility between populations are all behavioural: delayed marriage, use of contraceptives and induced abortion, and lactational amenorrhoea (which is a physiological determinant, but which is typically estimated in empirical demographic work by measuring the duration of breastfeeding [43]). Sociological demographers have also noted that such behavioural mechanisms are often the focus of cultural norms and have been interested in how variation in cultural norms influences fertility, particularly in natural fertility societies. For example, cultural norms for delayed marriage are thought to be the route through which historical Europe achieved fertility well below the physiological maximum, compared to norms which promote long periods of lactation and post-partum sexual abstinence, which kept fertility relatively low in sub-Saharan Africa [44]. These norms are assumed to act in the service of maintaining the physical health and economic well-being of children, mothers and the wider family, though only occasionally does such demographic work explicitly consider *why* different cultural norms should arise in different populations, or relate these cultural norms back to features of the local ecology (see [45] for an example).

The first wave of evolutionary research also made inroads into illuminating the behavioural regulation of fertility: two edited volumes were published between the late 1980s and mid 1990s which focused explicitly on human reproductive behaviour [46,47]. This work focused on how parental investment decisions determine individual-level variation in fertility. Such work has clear parallels in conventional demography. For example, historical demography has demonstrated how fertility responds at an individual level to economic conditions, under the assumption that marriage and fertility decisions will function to maintain the health and economic well-being of families [48–50]. Parental investment theory, an influential body of theory which has been developed in evolutionary biology, is a key theoretical framework for much work in evolutionary demography [51–54]. Socio-ecology and individual condition determine patterns of parental investment, which ultimately determines the total number of children produced. Parental investment decisions may include whether or not to invest in or continue investing in a particular child (e.g. infanticide and abandonment have both been common forms of disinvestment historically and cross-culturally), and how much to invest in a child (e.g. breastfeeding decisions and restricted sexual activity aimed at prolonging birth intervals). Much work during this period was produced by human behavioural ecologists, whose goal is to explain variation in human behaviour, including fertility behaviour, as a function of the socio-ecological environment [55,56]. For example, Mace [57] modelled how parental investment, specifically the costs of launching children successfully onto the marriage market, influenced the fertility of Gabbra pastoralists in northern Kenya (a society which requires bride price, or the transfer of resources from groom to bride's family at marriage). Her model suggested that in populations like the Gabbra, where heritable wealth pays a substantial role in determining offspring reductive success, maximizing fertility will not necessarily maximize long-term fitness (i.e. it pays parents to not just rely on physiological mechanisms to regulate fertility, but also use behavioural manipulation of fertility to avoid producing too many children). Such theoretical work is also supported by empirical evidence produced by historical demographers in both historical Europe and, particularly, Asia, that marital fertility is lower than would be expected from a purely physiological regulation of fertility, which suggests fertility control within marriage, which may function as a form of parental investment [58]. Further, anthropological demographers have recently produced qualitative evidence that couples in high-fertility populations consciously strategize about breastfeeding decisions and sexual activity in order to manipulate the length of birth intervals, and use local cultural norms flexibly in order to do so [59]. Their stated rationale for such behaviour is exactly as a life-history theorist would predict: to maximize the health of each child but also the mother so that she can conserve sufficient energy and health to manage her whole reproductive lifespan optimally.

(d) The demographic transition

Parental investment theory is based on individual- or couple-level cost-benefit analysis. One similarity between evolutionary and conventional demography is that both types of models consider such cost-benefit analysis to be a key factor in the fertility decline which occurs as part of the demographic transition. Economic factors have always been prominent in explaining the demographic transition, and individual cost-benefit models emerged as the dominant paradigm for explaining fertility decline in mid to late 20th century demography [13,60–62]. These micro-economic models assume that fertility started to decline as the costs and benefits of children changed with industrialization and mortality decline. Such models hinge on the intuitive notion of a trade-off between the quantity and the quality of offspring, and assume that parents gain more from investing in the quality of children over their quantity as mortality declines and populations develop economically. Evolutionary demographers have also proposed that the benefits of investing in the quality of children over quantity increase during economic development. Conventional demographers have often argued that fertility is kept high in pre-demographic transition populations because parents actually gain economically from producing children, who provide valuable labour to their parents and are also a secure

form of old-age insurance [62]. Evolutionary demographers, in contrast, assume that, though children may provide labour and thus offset their own costs to some degree, they are always a net economic drain on their parents, since evolutionary theory predicts that resources should always be used in the service of reproduction, and not vice versa. During the first wave, Kaplan [63] directly tested evolutionary versus demographic 'wealth flows' predictions about the economic value of children in pre-transition societies, and concluded that children never fully repaid their parents' investment (see also [64], but see [65]).

Evolutionarily speaking, it is a puzzle that industrialization is correlated with a decrease in fertility, as a simple prediction from life-history theory suggests that considerable increases in resource availability should be converted into additional offspring. A small but steady stream of first wave work on fertility decline was produced in an attempt to solve this puzzle. Turke [66] suggested that industrialization increased the costs of raising children, not just because raising children in such economies required additional expenses, such as education, but also because it changed the nature of childrearing. Throughout most of human history, childrearing was cooperative, with mothers, fathers, grandparents, and other family members cooperating to feed and care for children [67]. As individuals became more mobile as industrialization shifted the primary means of subsistence away from agriculture and towards market employment, family networks broke down. This made it harder to spread the costs of childrearing across extended kin, concentrating the costs of reproduction on the parents, which may have prompted a shift towards smaller families. Note, incidentally, that this idea that humans are 'cooperative breeders' was in part stimulated by evolutionary researchers asking why human fertility was so *high* (in contrast to the demographic heuristic that natural fertility rates are surprisingly low). We have more rapid reproduction than our closely related ape cousins: birth intervals are around 4–5 years for chimps and gorillas, and 8 years for orangutans, whereas ours tend to be in the range of 2–4 years [68]. This may be explained by our cooperative system of reproduction, largely absent in other apes [69,70].

This cooperative strategy of reproduction may partly explain why cultural norms and social learning seem to be so important in determining fertility behaviour (as conventional demography has so clearly demonstrated). We may be particularly sensitive to the behaviour of others, because the availability of support to help us reproduce was vital for successful reproduction throughout our history. It may also pay to base reproductive behaviour on observing the behaviour of others, rather than use a trial-and-error approach, because births are relatively rare and costly events, which leave little opportunity to learn from trial and error. Not only do cultural institutions (such as marriage and inheritance practices) influence our fertility by acting as part of our socio-ecology, but cultural norms (such as breastfeeding practices, sexual behaviour, and the acceptability of contraception) may play a more active role in explaining why fertility is so variable between individuals and populations, as they have the potential to change quite rapidly over time. Only a small fraction of first wave work showed an interest in cultural influences, however. The field of cultural evolution emerged during the 1980s as a subfield of the evolutionary behavioural sciences, which explicitly recognizes the importance of culture in determining human behaviour, but which also recognizes that cultural evolution may follow trajectories that are not tightly constrained by biological evolution [71–75]. A leading text in this work [72] tackled the demographic transition puzzle, suggesting that our cognitive biases towards emulating the rich and famous—or at least high-status members of our local social networks—may drive the shift towards low fertility. According to this account, once new means of gaining status emerged which competed with the production of children, then high status began to be associated with lower fertility than average, which could then have been copied by lower-status individuals via a process called 'prestige-biased' cultural transmission. Although such work provided novel theoretical explanations for the fertility decline, little empirical research was produced during the first wave to support or refute such cultural evolutionary explanations.

(e) The end of the first wave

In summary, the first wave in the 1980s and 1990s saw a considerable body of evolutionary research on fertility emerge that was largely focused on ultimate explanations of fertility as well as explaining within-population variation in small-scale, natural-fertility societies. Alongside this work were a number of papers aimed at explaining the fertility transition, both proposing evolutionary explanations for this apparent puzzle, and testing some of these models. Arguably, the culmination of the first wave of evolutionary demography is marked by three significant publications which provide useful summaries of the insights gained by this stage, laying a solid foundation for the research which would follow.

First, 1995 saw the publication of the landmark book '*Ache life history: the ecology and demography of a foraging people*', by the anthropologists Hill & Hurtado [76]. Summarizing the results of many years of field research among a population of South American foragers, the book remains one of the most in-depth studies of life-history decisions in a natural fertility population ever conducted. It followed in the footsteps of previous anthropologists who had produced thorough demographic accounts of small-scale societies [77], but by the mid-1990s both evolutionary theory and demographic methods were sufficiently advanced that Hill & Hurtado could produce an impressively comprehensive and sophisticated analysis of the life history of a particular population. Their work included attempts to understand the mechanisms underlying fertility variation (e.g. the relationship between nutritional status and fertility) and to assess evidence for the optimization of key life-history trade-offs, such as those between growth and reproduction and between fertility and child survival (see also [78] for a similar, though less comprehensive, examination of the evolutionary demography of an African pastoralist population from wave one). *Ache life history* was hugely influential, not least because it marked a shift towards increasing methodological sophistication as Hill & Hurtado capitalized on new statistical methods being developed in demography and other social sciences. It effectively demonstrated the potential of an evolutionary and ethnographically informed approach to yield insights into multiple questions about human reproductive behaviour.

Second, in 1996, Hillard Kaplan developed a comprehensive evolutionary model of fertility variation, incorporating evolutionary parental investment theory, the proximate determinants of fertility framework, and micro-economic

models of human capital inspired by the work of Gary Becker, to explain fertility variation across both traditional natural-fertility populations and modern low-fertility populations [79]. According to Kaplan, in small-scale societies similar to those in which our ancestors evolved, the returns to parental investment in an offspring's adult productivity reach diminishing returns relatively quickly, whereas in modern wage-labour economies returns to investment in offspring do not diminish until higher levels—particularly for those with higher levels of embodied capital in the modern form of education. In consequence, the psychology that had evolved to detect diminishing returns leads modern parents to invest more in a smaller number of children, with decisions to invest more in each child leading to a particular number of children. Modernization is also accompanied by novel conditions where offspring survival is virtually guaranteed and where few individuals have insufficient resources to reproduce, providing little check on the motivation for high child investments. Consequently, modern fertility declines below fitness-maximizing levels, but can nevertheless be understood as the product of previously adaptive mechanisms. Kaplan supported this 'maladaptive' hypothesis with data showing that fertility limitation in modern populations advances offspring educational attainment and adult income, but does not increase offspring survival or fertility [80]. In contrast, other evolutionary demographers at this time suggested that modern low fertility could in fact be adaptive provided that strong socio-economic advantages are transmitted across generations that safeguard future generations from levels of poverty or disease that would limit their reproduction (e.g. [81]).

Finally, in 1998, Monique Borgerhoff Mulder published a short but highly influential review of evolutionary explanations for the puzzling decline of fertility in the later stages of the demographic transition, which provided a useful summary of current thinking, encompassing Kaplan's model but also burgeoning insights in the field of cultural evolution [82]. Borgerhoff Mulder identified three main evolutionary hypotheses for this phenomenon present in the literature: low fertility could be explained (i) by life-history models which predict that in competitive environments investing in few high-quality offspring can be fitness-maximizing over the long-term; (ii) as a consequence of cultural evolutionary processes which may divert fertility away from fitness-maximization [72]; or (iii) by 'adaptive-lag' arguments which suggest that modern low fertility is the result of cognitive mechanisms that are out of step with modern environments (broadly, the category into which Kaplan's model falls). Borgerhoff Mulder's review set a clear agenda for future research then undertaken in the second wave, which subsequently placed focus on both testing mutually exclusive predictions of these alternative hypotheses, and/or worked to integrate their complementary aspects.

All three of these publications also clearly identified the need for evolutionary demographers to further develop theoretical accounts beyond fitness maximization models to provide a comprehensive explanation of why fertility varies so dramatically between and within populations. In fact, despite the common assumption by evolutionary demographers that fertility maximizes fitness in natural-fertility populations, the possibility began to emerge from the latter stages of first wave work, including Hill & Hurtado, that fertility even in natural-fertility populations may be lower than would seemingly maximize individual fitness [83]: the few direct tests of the hypothesis that fertility maximized fitness found that the women who had produced the most children in a particular population also had the highest fitness. This suggests that the majority of women in that population who were not reproducing at the maximum fertility were not maximizing fitness, which leads to the question of why they did not produce more children. This conclusion set up a variety of challenges, which are subsequently being taken up in the second wave of evolutionary research on fertility. One challenge was to determine if fertility rates do, in fact, maximize fitness in natural fertility populations and if so, then what was wrong with first wave measures of fitness (were they too short-term, or missing some vital component, such as not taking sufficient account of individual variation in state, or condition?). And if observed fertility rates do not maximize fitness, then why not, and what is a better model of fertility variation? This leads to the need for models that integrate explanatory hypotheses with a more detailed understanding of proximate factors affecting fertility. As we describe below, the second wave has responded to these challenges, both by expanding consideration of the factors influencing fertility at proximate and ultimate levels, and by methodological and theoretical advancements refining the measurement of fitness and our understanding of adaptation.

3. The second wave

This volume highlights emerging research in the second wave of evolutionary demographic research on fertility, reflecting developments since the late 1990s. If the first wave focused heavily on interpreting fertility in terms of fitness maximization, the second aims to develop a broader understanding of fertility variation (without losing sight of the evolved nature of human physiology and behaviour), which includes (1) a much greater focus on the psychological and cultural mechanisms underlying fertility variation, (2) a more explicit recognition of the complexity and multi-causal nature of fertility variation, (3) greater emphasis on fertility decisions in developed nations and low-fertility populations (see also [84]), and (4) greater methodological sophistication, including multigenerational, cross-cultural, and comparative research. These trends involve, and require, evolutionary demography to engage more actively with the wider demographic literature. The study of low-fertility societies, for example, largely absent from first wave research, can build on the very substantial body of demographic work on this topic (see [85] for a review). In the subsections below, we highlight key trends as exemplified by the papers in this issue.

(a) Optimizing offspring

As described above, the first wave made significant steps into identifying and addressing the evolutionary puzzle of the demographic transition. A distinguishing feature of the second wave has been the further elaboration of these explanations, adding complexity and new and more sophisticated empirical tests of existing hypotheses, and in some cases challenging and re-examining certain stylized facts about the nature of demographic transitions more or less commonly accepted during the first wave. For example, until recently, debate concerning whether or not modern low fertility can be considered fitness-maximizing across the long term has been

thwarted by the lack of multigenerational analyses capable of tracking the long-term impacts of fertility limitation. Goodman *et al*. [86] recently resolved this debate by compiling data across four generations of a Swedish-born cohort born during the demographic transition, including not only data on descendant mortality, fertility, and success of the marriage market, but also school test performance, educational progression and adult income. They confirmed Kaplan's proposal [79,80] that fertility limitation is associated with notable and far-reaching benefits to descendant-embodied capital in the form of socio-economic success, particularly among initially wealthy lineages, but has little impact on descendant reproductive success. These results suggest mathematical models showing that low fertility could hypothetically maximize individual fitness across the long term in modern settings are unrealistic [81,87].

Following in this vein, our special issue begins with four papers that revisit some of the dominant themes of the first wave in the light of theoretical and empirical developments. Kaplan's [79] model of fertility variation focused on how changes in the way in which humans produce wealth can prompt fertility decline. Shenk *et al*. [88] develop these ideas further, specifically by adding an extra layer in terms of status, defined as relative social rank within a society. Status was not ignored in first wave work, given it is closely linked to resource availability [81,89–91], but newer models [87,88] draw strongly on insights from a larger empirical literature in evolutionary demography including new research on status in small-scale societies (e.g. [92,93]) and are also able to use modern computational power to more extensively explore the parameter space of models. Shenk *et al*.'s model allows parents to optimize investment in both the embodied capital (defined on an absolute scale) and the status/rank of their offspring (defined relative to others). The model finds that in conditions common in demographic transition societies, parents are predicted to increase investment in both embodied capital and social status, with each type of investment leading to separate and significant decreases in fertility, particularly under conditions of high inequality and intense status competition. Such models may help explain why fertility decline gets started with the shift towards modern market economies, why it is maintained under such ecological conditions, and why fertility decline might deepen if economic development leads to greater inequality or status competition.

Stulp & Barrett [94] also consider the relationship between wealth and fertility in modern populations—long considered the 'central theoretical problem of sociobiology' [95]. While first wave research clearly showed a positive relationship between wealth and fertility in natural fertility populations, influential papers in the late 1980s and early 1990s suggested that the relationship between wealth and fertility switched during the fertility transition to become negative [95,96]. Evolutionarily, this is hard to explain, as individuals are predicted to use their resources in the service of increasing their reproductive success. Here, Stulp & Barrett question the validity of the cross-sectional samples used to assess the relationship between wealth and fertility, particularly those presented in the influential articles of Pérusse [96] and Vining [95]. They find that even in post-transition societies, fertility is still largely positively correlated with wealth when longitudinal datasets are appropriately analysed. They note, here and elsewhere, that these relationships are complex, however [97,98]. They may be stronger for men than for women and may vary between groups within complex societies (such as different ethnicities), suggesting that it is important to not treat modern complex societies as a uniform whole, but to address, and use, variation within societies when testing evolutionary hypotheses. They further question the assumption that the wealth-striving behaviour of humans in industrial population reflects the distortion of a universal evolved predisposition, and suggest that much economic behaviour can be better interpreted in terms of risk management and reduction. They also caution that a broadly positive relationship between wealth and fertility does not mean that post-transition societies are maximizing their fertility, and urge that careful attention must be paid to the origin and historical trajectory of social institutions (i.e. their cultural evolution) when trying to explain the fertility transition. For example, institutions can make a significant difference to the costs and benefits of children, as they illustrate with child labour laws: legislation keeping children out of the labour market (or in it) substantially influences the costs and benefits of raising children. Understanding how such legislation comes into being is therefore an important part of understanding variation in fertility, often neglected by evolutionary demographers.

Lawson & Borgerhoff Mulder [99] revisit the notion—common to both evolutionary and economic demography—that variation in fertility can be understood as the optimization of a trade-off between offspring quantity and quality. They highlight ways in which simple fitness-maximization models built on this foundation, while useful heuristically, poorly reflect the complex reality of fertility decisions. Reviewing the literature on quantity–quality trade-off effects in traditional populations characteristic of our evolutionary past, they then put forward the argument that while the optimization of the quantity–quality trade-off may be fundamental in defining the upper limits of human fertility and the shared features of human reproductive physiology, trade-offs between reproductive and somatic effort and between fertility and mating effort, probably play a more pivotal role in accounting for fertility variation in settings characteristic of our evolutionary past. They argue that the trade-off between the perceived quality and quantity of offspring is more obviously relevant to individual decisions to reduce fertility in modern low-fertility populations. Yet, just as this trade-off becomes relevant, fertility behaviour apparently becomes maladaptive, yielding no apparent benefits in terms of long-term reproductive success [50]. With little indication of the tactical balancing of the quantity–quality trade-off in pre-demographic transition environments, Lawson & Borgerhoff Mulder suggest the demographic transition presents a potentially radical shift in the nature of reproductive decision-making. This is a conclusion that raises interesting questions about the flexibility of human behaviour in rapidly changing environments, and highlights the need for more a sophisticated understanding of the proximate mechanisms underlying human reproduction.

One conclusion from Lawson & Borgerhoff Mulder [99] is that models of fertility, in both pre- and post-demographic transition contexts need to better incorporate the complexities of sequential reproductive bouts and sexual reproduction. One complexity often lacking is the need to incorporate both reproductive partners in fertility decision-making. Men do sometimes appear in demographic accounts of fertility, though conventional demographic research traditionally

focuses heavily on women, as noted in one review article: 'Demography has regarded men as important economically but as typically uninvolved in fertility except to impregnate women and to stand in the way of their contraceptive use' [100, p. 83]. This quote also illustrates a long-standing assumption among many demographers that men may be responsible for high fertility in some situations, as they dictate reproductive decisions and exploit female labour by insisting on large families. Some evolutionary researchers have similarly considered that men may have higher fertility desires than women, based on theoretical expectations of sexual conflict between men and women, such that men may benefit from pushing women into rapid reproduction which may endanger women's own health.

Moya *et al.* [101] examine these evolutionary claims closely and use theoretical models to show that universally higher fertility preferences among men as compared to women is unlikely to be explained through evolutionary sexual conflict. Only in specific circumstances where men can remarry quickly and easily, and without substantial costs, are male fertility preferences high enough to risk wearing out their first wife with excessive childbearing likely to evolve. Such conditions are relatively rare, though particularly high 'quality' men, who are very attractive on the marriage market, may be able to repartner quickly. This article also calls for evolutionary social scientists to build more precise models of reproductive decision-making. Firstly, if sexual conflict is to be used to help explain fertility, then the precise conditions that are required for this sexual conflict to arise need to be carefully specified (Moya *et al.*'s models even show that women can prefer higher fertility to men under certain circumstances). Secondly, they show that fitness maximization arguments are unlikely to explain the empirical observation that men do have higher fertility preferences than women in the majority of those populations where the sexes differ (and often the sexes are in agreement), so that other factors, such as misfiring psychology, which is out of sync with modern environments, or cultural evolution need to be incorporated in understanding sex differences in fertility intentions.

All the papers in this section continue the first wave focus on understanding the ultimate explanations for fertility variation, since none directly investigate proximate mechanisms. All, however, conclude that fitness-maximization arguments, while useful, cannot fully explain fertility variation; that more complex models, incorporating several different dimensions of fitness maximization are necessary; and that the proximate mechanisms need to be examined much more closely in evolutionary work in order to understand how and why fertility deviates from fitness maximization, since even the most complex, multi-dimensional fitness-maximization model is very unlikely to be able to explain contemporary low fertility.

(b) Getting a better handle on behavioural mechanisms

Second wave research has begun to show a more dedicated interest in the behavioural determinants of fertility, and not just those related to parental investment decisions. Hruschka & Burger [102] clearly demonstrate the importance of understanding behavioural mechanisms to interpret fertility in low fertility societies. They use a simple statistical method to explore how *variance* in fertility changes over the demographic transition in order to shed light on the key determinants of individual and population differences in fertility. Their analysis of Demographic and Health Survey Program data suggests, somewhat provocatively, that the vast majority of fertility variation within high-fertility societies is simply due to random timing of events—or at least, their results suggest that this is the most parsimonious explanation. This implies that within many populations, between-individual differences in neither physiological condition nor behavioural regulation of fertility make as much of a difference to the number of children women produce as it is often thought that they might. This is most notable in high-fertility societies as well as many societies in the midst of fertility transitions. In contrast, their analysis suggests that in the small number of low-fertility societies examined in their analyses, women are aiming at a limited number of targeted family sizes, consistent with the view that there is tighter behavioural control over fertility in such populations.

The psychological mechanisms underlying fertility decision-making are remarkably understudied, in any discipline. McAllister *et al.* [103] here provide the first comprehensive review of the interdisciplinary literature that does exist on this topic. These authors draw together the theories which are beginning to spring up to explain reproductive decision-making. These are diverse, including life-history theory from evolutionary biology [104], attachment theory [105] and terror management theory [106] from psychology, and the theory of planned behaviour [107], which is increasingly being used in demography, building on limited interest in the psychology of fertility in earlier work in this discipline [108–110]. They then review the empirical literature which has used these theories as frameworks to direct empirical research. The benefits of social psychology methods, especially the experimental manipulation of fertility preferences in the laboratory, are contrasted against their use with rather biased samples, such as university students. However, such work does suggest that psychological mechanisms may mediate variation in fertility between individuals and populations. For example, experimental work has suggested that cues to childhood stress, father absence, and mortality all lead to predictable shifts in fertility preferences. This review also suggests that personality may mediate fertility behaviour, though in complex ways: the relationship between personality and fertility differs between men and women [111], and also cross-culturally [112].

This psychological work is so far rather fragmented. It is dispersed across several fields, which use different theoretical models, and which have not so far integrated well with one another. This research has also so far been conducted exclusively on high-income, low-fertility populations; only ethnographic, qualitative evidence is available from higher-fertility populations on the cognition underlying reproductive decisions. This area is therefore ripe for further research. We hope that McAllister's valuable review article will stimulate greater interest in, and multi-disciplinary development of, this area of research on the psychological mechanisms which underlie reproductive decision-making.

Alongside the glimmerings of an interest in psychological mechanisms has been the more substantial development of the field of cultural evolution of fertility. Colleran [113] provides the first review of cultural evolutionary hypotheses of fertility. There has been considerable emphasis in the conventional demographic literature on the importance of cultural norms, including consideration of how social influence may influence fertility decisions via social networks (e.g.

[114–116]). But there has been little cross-fertilization so far between this literature and evolutionary approaches to culture. Such cross-fertilization could be useful because there has been little formal theory in the demographic work on cultural influences on fertility; cultural evolutionary approaches can therefore provide a much-needed set of formal models from which new predictions can be derived. Colleran's review echoes the theme emerging from second wave research that multi-causal explanations for fertility are essential. She argues that cultural evolution approaches need to be integrated with other approaches to fully understand fertility variation;—there has been a tendency in both evolutionary and conventional demography for work on economic models of individual cost-benefit analysis and cultural models to develop in parallel rather than together. Yet neither cost-benefit analysis nor cultural influences act independently of one another, as Colleran highlights by emphasizing conceptual overlaps between cultural evolutionary models and human behavioural ecology: cultural evolutionary models, for example, do include cost-benefit analysis as just one of a suite of psychological adaptations for learning about environmental and other cues. Cultural evolutionary research emphasizes the coevolution of economic and cultural systems and uses a multilevel approach, which recognizes that individual strategies for adaptation within groups and competition between groups often co-occur (e.g. [117–119]). Colleran specifically recommends closer attention be paid to the distinct processes which lead to the origin, spread, and maintenance of fertility decline.

The evolutionary research on psychological mechanisms and cultural evolution has so far been somewhat distinct, yet these two fields are clearly closely related (as has been recognized in other second wave work, e.g. [120,121]). While reproductive decision-making will involve individual cost-benefit analysis, cultural factors will influence these calculations in a variety of ways. Arguably, conventional demography is ahead of evolutionary demography here: theories which have recently been incorporated into demographic models of reproductive decision-making, the theories of planned behaviour [122] and conjunctural action [123], take into account both individual characteristics and social influence. In this issue, Bentley *et al.* [124] take a step forward for the evolutionary sciences by combining individual decision-making and social influence in their theoretical model of reproductive decision-making. Their model incorporates both the information on which individuals base their decisions (specifically, how transparent are the costs and benefits of decisions), and the recognition that an individual's decisions are contingent on social influence to a greater or lesser degree. The authors then identify ways in which these two dimensions of transparency and social influence may interact to produce different domains of decision-making relevant for different types of reproductive decisions.

(c) Developmental influences and reproductive timing

One relatively neglected aspect in conventional demography is the influence of early-life environment on fertility. We are a long-lived species with a long childhood, and much of the social learning which influences our later behaviour is developed during childhood. Developmental influences on fertility were not ignored in first wave demographic research [125–128]. Much of this literature, motivated by life history theory, examines whether the childhood environment canalizes our reproductive trajectories into either 'fast' or 'slow' life histories/courses. This literature hypothesizes that growing up in a poor environment kickstarts a fertility strategy which involves early sexual debut and first reproduction as well as rapid subsequent reproduction with resulting high fertility. In contrast, a benign environment is predicted to lead to later reproduction (so that individual capital can be built up before reproducing), slower reproduction (because the chances of both self and children surviving are higher), a smaller number of children born overall, but not necessarily more surviving children. Early-life environment has not been entirely neglected in conventional demographic approaches. This life-history work has parallels with the 'weathering hypothesis' in the demographic literature, which argues that growing up in poor environments means that first births should be early so that women can reproduce while they (and their mothers, whom they rely on for childrearing help) are still healthy [129,130]. The weathering hypothesis tends to be restricted to explaining ethnic differences in childbearing in the US, however, and has not been widely used outside this context. Life-history models, in contrast, can be generalized across different contexts to explain fertility differences across socio-economic strata.

Coall *et al.* [131] provide the first review of the evidence that childhood experiences influence subsequent fertility outcomes. There is suggestive evidence that stressful childhood environments lead to earlier reproductive development and timing [132]; however, the evidence is lacking on whether early-life environment influences fecundity and fertility in later life (but see [133]). Therefore, the evidence regarding whether early stress results in women having higher numbers of children overall is inconclusive. Further, the influence of early environments on fertility has almost exclusively been studied in high-income, low-fertility populations (for an exception, see [134]). In populations which are resource-stressed, it may be that growing up in harsh environments delays, rather than accelerates, first reproduction, because of the constraints imposed by very low access to resources [127]. The mechanisms which result in early stress leading to earlier reproduction have also not been studied in detail. In their review, Coall *et al.* focus on the physiological mechanisms which may mediate these relationships and suggest potential roles for birth weight, childhood body composition, risky health behaviours, and developmental influences on attractiveness. Again, this is an area in its infancy that has good prospects for subsequent investigation.

As this review clearly demonstrates, there is a large body of research on age at first birth in evolutionary demography. This is a key reproductive decision in evolutionary biology, as it marks the life history shift from growth to reproduction. As noted by Towner *et al.* [135], however, age at last birth has received relatively little attention. While there has been some relevant work in the historical demography literature, it is the least well studied of all the components of fertility (age at first birth, length of birth intervals, age at last birth, and childlessness). In evolutionary demography, the literature has been dominated by interest in the evolution of menopause [136]. Though we have concentrated in this review on individual variation in fertility, one of the successes of first wave evolutionary demography was to consider how evolution has shaped our species-typical life history. In particular, influential work was produced suggesting that menopause, a life-history

trait almost unique to humans, may have evolved because of our cooperative system of reproduction: the grandmother hypothesis suggests older women benefit more from investing in existing children and grandchildren than continuing to produce children of their own [136,137]. Towner *et al.* refocus evolutionary attention on individual variation in age at last birth. They provide clear evidence in their review of the literature, and their Bangladeshi case study, that age at last birth typically precedes menopause by a decade or more. This begs the questions: why stop early?; and does stopping early represent an important strategic behaviour in fertility decision-making? Towner *et al.* also review both the proximate and ultimate explanations for variation in age at last birth, and suggest this is another area ripe for research in evolutionary demography.

(d) Emerging trends

The final three papers in our volume reflect notable emerging trends where we are particularly keen to see continued development. As we have described above, second wave research has maintained an interest in understanding variation within high-fertility populations, but has also become increasingly interested in the demographic transition and in low-fertility settings. As part of this trend, one particularly welcome development is the growing body of field studies on 'transitioning' populations currently undergoing economic development and the fertility decline [138–140]. This includes research into the uptake of modern contraceptive technology, which has now been analysed both in terms of its consequences for child health and in relation to cultural transmission [141–144]. There have also been a number of studies examining how parents navigate parental investment decisions when faced with (evolutionarily) novel conditions, such as sudden declines in child mortality [145] or the rapid increases in opportunities to invest in formal education [146,147]. We encourage further research of this kind because it is only by focusing our attention on populations actively undergoing substantial economic development that we are likely to achieve a comprehensive understanding of how reproductive decision-making changes as populations modernize. Such research also provides an opportunity to provide a more precise understanding of adaptive lag in fertility decisions, which most researchers now agree is fundamental to evolutionary explanations of the demographic transition—but is rarely studied directly. Finally, this work offers opportunities for more active engagement with the policy-orientated focus of many conventional demographic researchers interested in better understanding how populations may be encouraged to alter reproductive behaviours to the benefit of maternal and child health.

Another trend we are keen to promote is comparative research. Comparative research offers potential for rigorous testing of hypotheses for why fertility varies between populations. The second wave is beginning to produce such work [148,149]. Such empirical work is enabled by the increasing availability of data across the full spectrum of human populations, and the increasingly high quality of datasets, including multigenerational datasets [86,150,151]; along with advances in statistical techniques in the social sciences, which can be used to analyse such large and complex datasets. Snopkowski *et al.* [152] illustrate trends in both comparative work and field research on transitional populations. The authors examine education, a strong negative predictor of fertility cross-culturally, which has received considerable attention by demographers [153]. Snopkowski *et al.* examine five pathways through which education is posited to affect fertility, performing the same analysis across three populations moving through the fertility transition. They find some commonalities and also some differences across societies, suggesting both that education is probably such an important predictor of fertility cross-culturally because it operates through multiple causal pathways, but also that these pathways may be turned on or off (or tuned up or down) in different socio-ecological circumstances. Such comparative research offers exciting possibilities to rigorously test hypotheses, informed by the detailed anthropological knowledge of researchers who have collected these datasets or worked in these populations. This complements comparative work more widespread in conventional demography, using databases such as the Demographic and Health Surveys, which has the advantage of larger sample size and more populations to compare, but the downside of less-detailed ethnographic knowledge (such that some variables may not be appropriate or easily interpretable, and other key variables may be missing) and less-homogeneous populations (such that analyses are vulnerable to the ecological fallacy, i.e. erroneous inferences made from aggregated data which misrepresent relationships between variables within communities or ethnic groups) [154,155].

Recent years have also witnessed renewed interest in how best to measure fitness and in using demographic data to assess how selection is currently acting on the human phenotype, particularly in modern post-demographic transition settings. Mortality has been reduced to such low levels in many parts of the world, and postponed almost entirely into old age, that differential mortality may no longer be very important in driving natural selection. Differential fertility may now be the primary engine of natural selection in post-demographic transition societies [156]. This raises the question of how best to measure fitness, since different measures can come up with different results (see [157,158] for an example of different measures of fitness resulting in exactly opposite conclusions using the same dataset). In this issue, Ewbank [159] highlights that reproductive timing matters (see also [160,161]), as failing to take into account the generational nature of reproduction may lead to the mismeasurement of fitness, particularly in humans and other long-lived organisms. Short-term measures of fitness may also be overly sensitive to the failure to reproduce, yet childlessness is found in nearly all human societies and has become quite common post-demographic transition. This means we need to move beyond simple 'baby counting' and attempt to acknowledge and incorporate population-level demographic processes in a more formal manner than has been common in evolutionary demography. There is also clearly a need for evolutionary demographers to incorporate indirect fitness into their models, since our cooperative system of reproduction means that indirect fitness may be particularly important in our species (indirect fitness is achieved not through one's own reproduction but through that of one's genetic relatives).

Finally, Burger & De Long [162] end our issue with a number of potential avenues for future research, by making predictions about how fertility may change in the future. They speculate that the very low and below-replacement-level fertility which characterizes high-income populations may not be permanent (see also [163]). In contrast to the assumption of demographic transition theory that fertility

only ever falls once it begins to decline, fertility decline has previously reversed during the baby boom of the 1960s, and a number of very high-income populations have seen recent upticks in fertility [14]. Burger & De Long have several suggestions for those predicting future trends in fertility. First, models should take into account the possibility of natural selection increasing the frequency of traits associated with high fertility; natural selection, after all, operates on fitness and individuals with few or no children leave fewer genetic contributions to future generations. It is also possible that cultural norms may spread which are associated with higher, rather than lower, fertility. The authors argue that high levels of wealth inequality, both within and between societies, may result in fertility remaining high in less-well-resourced populations and sub-populations (a finding consistent with that of Shenk *et al*. [88]). Finally, Burger & De Long suggest that changes in cultural institutions that allow women to meet the high opportunity costs of reproduction they face in modern market economies (such as paid maternity leave and affordable childcare) may also contribute to increases in fertility.

4. Conclusion

Evolutionary demography assumes that understanding that our physiology, psychology, and behaviour have evolved over time through the process of natural selection allows insights into why fertility varies so widely, and how such variation arises from local social and environmental contexts. We have argued that the first wave of evolutionary demography focused on testing hypotheses derived from the core principles of an evolutionary framework, specifically that variation in fertility can be interpreted as adaptive variation which functions to optimize reproductive success in various socio-ecological settings. While this proved a useful heuristic in understanding some aspects of fertility, such as age at first birth and length of birth intervals, conclusive evidence that total fertility is fitness-maximizing in natural-fertility societies was not forthcoming. First wave research also suggested that fertility decline probably cannot be interpreted as adaptive, though it may be influenced by psychological and cultural mechanisms which were adaptive in previous environments. The second wave, in contrast, focuses on fleshing out evolutionary demographic models to deal with the complex reality of fertility behaviour, as well as more meaningfully integrating our work across populations, evolutionary subfields, and neighbouring disciplines. All papers in this volume tackle head-on the complexities involved in analysing fertility, particularly the transition from high to low fertility which universally seems to follow, or occasionally co-occur with, mortality decline and economic development. The second wave is thus energetically investigating the unanswered questions from, and attempting to meet the challenges revealed in, the first wave. This is an exceptional time in the history of the evolutionary social sciences in general, and evolutionary demography in particular, with increasing acceptance and wide publication of research from the evolutionary human sciences in evolutionary biology, general science, and social science journals. We expect that the next decade or two are likely to bring even greater methodological sophistication, including significantly more comparative and cross-cultural work, and greater theoretical integration with the social sciences. In the coming years, we hope to see evolutionary demography increasingly integrated in the conversations and journals of conventional demography and other social sciences, as we believe that the methodological rigour of demography and the theoretical clarity of evolutionary biology make a powerful combination.

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Endnotes

[1]We will follow social science usage in referring to the production of children as fertility, and the ability to conceive as fecundity, in contrast to biology, which reverses the meaning of these two terms.
[2]'fertility rates' refer to 'total fertility rates', a population estimate of the number of children expected for a women surviving throughout her reproductive years (assumed to be 15–49 years of age in the demographic literature) given current age-specific fertility rates.
[3]http://ec.europa.eu/eurostat/documents/2995521/6829228/3-13052015-CP-EN.pdf/7e9007fb-3ca9-445f-96eb-fd75d6792965.
[4]A simple example of the difference between proximate and ultimate explanations can be illustrated with the question, 'why do we eat?'. A proximate answer to that question is: we eat because we feel physiological sensations which tell us that we're hungry. An ultimate answer is: we eat because if we did not regularly take in food we would die, and dying tends to dramatically reduce evolutionary fitness.

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